

# The Systematics of the Charaxidae (Lepidoptera: Nymphaloidea)

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(Continued from p. 316)

## (7) Subfamily ANAEINAE

Anaeidi (Reuter, 1896).

(Type-genus: *Anaea* Hübner 1819, *Verz. bekannt. Schmett.*, pt. 3, p. 48; type-species: *Papilio troglodyta* Fabricius, 1775).

The Anaeinae to date comprise the following genera: *Anaea*, *Hypna*, *Polygrapha*, *Consul*, *Memphis*, *Cymatogramma*, and a new genus to be described later, all of which Comstock (1961), as we have seen, lumped together as subgenera of his omnibus genus "Anaea", together with *Siderone*, *Zaretis*, and *Coenophlebia*; but the last three genera I have placed in a subfamily of their own (the Zaretidinae) for reasons already stated. As pointed out by Comstock (1961, p. 5), the genera comprising the Anaeinae can be subdivided into two main sections on the basis of the wing-venation, i.e. in *Anaea* and *Hypna* the third subcostal vein (V.9) of the forewing arises from the common stalk basad of the fifth subcostal vein (V.7), whereas in *Polygrapha*, *Memphis*, *Cymatogramma* and *Consul* the third subcostal vein arises distad of the fifth. In *Anaea*, moreover, the fourth and fifth subcostal veins (Vs. 8, 7) of the forewing are much shorter than their common stalk; while in *Hypna* and the others these two veins are as long as, or much longer than, their common stalk, and the fourth subcostal vein (V. 8) tends to end in a downward curve in the costa, or in the apex of the forewing. As in the Ethiopian Euxanthinae, there is a marked tendency among the Anaeinae for some of the subcostal veins of the forewing to anastomose with the costal vein, or the first subcostal vein to be atrophied or absent. In *Anaea troglodyta*, for example, the first subcostal vein is usually absent, while in *A. aidea* it is vestigial. In *Cymatogramma echemus* the first subcostal vein is usually absent too, but in several species of the latter genus, i.e. *C. morena* (Hall) and *C. artacaena* (Hewitson), the first subcostal vein arises from the second subcostal vein near its base, joining the costal vein as a very short cross-veinlet. In nearly all the Anaeinae the first three subcostal veins anastomose with, and reinforce, the costal vein (V.12) which thus gives the appearance of continuing in its course almost as far as the apex of the wing, sending off several short veinlets to the costa on its way. In the atypical *Polygrapha cyanea*, however, the subcostal veins do not anastomose with the costal but run free, the third subcostal vein terminating at the apex of the wing, and the fourth ending with a downward curve in the outer margin below the apex as in *Charaxes* and *Prepona*. In addition, in *P. cyanea*, veins 5 and 6 of the forewing arise from a

common stalk beyond the apex of the cell, and in this respect resemble to a certain degree the aberrant venation of *Coenophlebia*. The wing-venation and the male genitalia of almost all the species of the Anaeinae have been figured by Comstock (1961), from an examination of which one can see that the Anaeinae are not a particularly homogeneous subfamily.

The genera comprising the Anaeinae will now be dealt with one by one, beginning with *Hypna*. The latter genus has been grouped with *Anaea* and its allies by various authors since the days of Westwood (1850-2). Comstock (1961) considered it to be but one seasonally dimorphic, polytypic species; but Röber (1916) divided the genus into three distinct species, i.e., *clytemnestra* Cramer, *rufescens* Butler, and *iphigenia* Herrich-Schäffer. The male genitalia of *clytemnestra* have been figured by Comstock (1961, fig. 122); the genital armature is distinctive, the tegumen being relatively short, the uncus heavily sclerotized and broad at its base (as in *Cymatogramma*), with the gnathos produced ventrad and medially bridged by a lightly sclerotized lobe. The valve is short and rounded at its apex, and the aedeagus is somewhat stout and irregularly toothed terminally. The saccus is relatively long and slender. If one compares the male genitalia of, say, *corumbaensis* Talbot with that of *iphigenia* or *clytemnestra* one can see some marked differences in them, the aedeagus in *corumbaensis* being shorter and stouter than in *iphigenia* or *clytemnestra*, the gnathos being broader and longer than in the latter two species, and the valve more slender and less broad at the apex. From the foregoing, it would seem that *Hypna* consists of a number of good species, not just one polytypic species. The early stages (already described above) and the imagos of this genus are sufficiently distinct from the other members of the Anaeinae to warrant my giving the group a tribe of its own, i.e. *Hypnini tribus n.*

Next, the genus *Consul*. Comstock (1961) placed in this genus (which is based on *Papilio fabius*) *Anaea pandrosa* Niepelt, "*Paphia*" *panariste* Hewitson, "*P*" *jansoni* Salvin, "*P*" *electra* Westwood, and "*P*" *excellens* Bates, mainly on the distinctive bifurcate gnathos that is present in the males of these species. The butterflies of this genus are relatively large in size, with the outer and inner margins of the forewing straight, and with the apex of the wing produced (except in the type-species *fabius* in which the wing is produced at vein 4), the hindwing being somewhat angular and strongly tailed at vein 4 in both sexes. In *pandrosa*, *panariste*, *jansoni*, *electra*, and in *excellens* (but not markedly so in *fabius*), the hindwing is also produced into a lobe at the anal angle. In *fabius*, and in *excellens*, the mid and hind tibiae and tarsi are heavily spined above and below; the tarsus of the foreleg of the females of some species of this genus (e.g. *fabius*) has a single claw; the palps typically are markedly porrect; and in addition, the special triangular scales near the base of the underside of the forewing are delimited by vein 1, not extend-

ing into space 1b as they do in *Anaea*, *Cymatogramma*, *Memphis* and *Polygrapha*. (In *Hypna* these specialized scales are also limited mainly to space 1a, but a few scales are found in space 1b, so that *Hypna* in this respect is closer to *Consul* than to the other genera.)

Of the genera comprising the *Anaeinae*, Comstock (1961) considered *Anaea* itself to be the most specialized one. He stated, on p. 38, that the genus, which is not a dominant one, was possibly of very ancient origin, and "the highly specialized gnathos somewhat suggests a relationship to the genus *Prepona*". As already stated above, Comstock resurrected the genus *Memphis* (which included *Cymatogramma*) for a large section of the *Anaeinae*, dividing the former into eight main groups, with a number of subgroups, on differences chiefly in the shape, colour and venation of the wings. He stated on page 56 that, "Judged by the facies only of the considerable number of species included in the subgenus *Memphis*, it could be suggested that there are a number of diverse elements lumped in an omnibus subgenus"; but he was of the opinion that the diversity of appearance of this genus was not supported by important structural differences. However, I myself think there are, in fact, sufficient anatomical differences by which it is possible to split *Memphis* into several genera. For example, in *Cymatogramma echemus* Doubleday the male genitalia (see Comstock, 1961, fig. 167) are more specialized than in *Memphis*, in that the aedeagus is relatively short and spindle-shaped, the uncus having its base expanded on either side into a pair of alae, and the gnathos with heavily sclerotized terminalia, and the valves relatively long and narrow. The venation of the forewing of *Cymatogramma* differs from *Memphis* too, in having the first subcostal vein of the forewing absent or vestigial; and the shape of the wing of *Cymatogramma* also differs from *Memphis* in having the inner margin more or less straight, not so markedly emarginate or hooked at the tornus as it is in *M. odilia*. In addition, *C. echemus* differs from *M. odilia* in having the the mid and hind tibiae and tarsi spined above and below, whereas in *Memphis* these structures are only spined below. There is also a difference in the forelegs of the males of *Cymatogramma* and *Memphis*, as well as in *Anaea*. The tarsus of the foreleg of *Anaea troglodyta*, for example, is small, stubby, densely hairy, less than half the length of the tibia, and is bluntly conical in shape; while in *C. echemus* the tarsus is longer than in *Anaea*, being less hairy and more slender, and tapers to a point, and is only slightly shorter than the tibia; and in *M. odilia*, although the tarsus is also slightly shorter than the tibia, it is obtusely rounded at the end, the foreleg as a whole being a larger, stronger structure than in the last two genera. There is also a marked difference in the larvae of these three genera, as has already been noted. So, with one eye to the butterfly and the other to the larva, it seems expedient here to separate the latter genera from one another, and also the red

species of Comstock's "*Memphis*" (centred around *Anaea phidile* Geyer) from the blue ones (centred around *M. odilia*).

(It should be mentioned, in passing, that the genus *Euschatzia*, which Grote (1898, p. 39) invented as a replacement name for Schatz's (1892) invalid genus "*Anaea*", is being treated here as a synonym of *Memphis*.)

For the red *Anaea phidile* I propose to erect the following genus, namely:—

FOUNTAINEA *genus n.*

(Type-species: *Anaea phidile* Geyer, 1834-7, *Zuträge Samml. exot. Schm.*, vol. 5, p. 27, No. 453, figs. 905, 906). This genus is named in memory of Miss M. E. Fontaine, some of whose drawings of the early stages of Neotropical Charaxids are reproduced in this paper.

*Fontainea* differs from *Memphis* (based on *Papilio odilia* Stoll) in having the inner margin of the forewing straight, not emarginate at the tornus; the third subcostal vein (V.9) arising relatively more basad than in *Memphis*; the palpus not unicolorous below, but with alternate dark and light longitudinal stripes, with the basal sensory patch triangular in shape, not somewhat quadrate as in *M. odilia*; the foreleg of the males shorter and more slender than in *Memphis*, with the tarsus tapering to a point, not obtusely rounded at the end as it is in *Memphis*; the male genitalia with a shorter tegumen and uncus, and the valves relatively longer and narrower than in *M. odilia*, and the sacculus with an apical hook; the larva (see fig. 11) being naked and papillated, not hairy or bristly as in *Memphis porphyrio* (fig. 13) or *M. morvus* (fig. 14).

The *Anaeinae* can be subdivided into a number of tribes as follows:—

- (1) The third subcostal vein (V.9) of the forewing arising basad of the fifth subcostal vein (V.7) ..... 2
- The third subcostal vein (V.9) of the forewing arising distad of the fifth subcostal vein (V.7) ..... 3
- (2) All subcostal veins of the forewing present; the first and second subcostal veins anastomosing with the costal; the third, fourth, and fifth subcostal veins long and running free; palps somewhat porrect; basal triangular scales on underside of forewing mainly below vein 1; the butterflies being large in size, with a broad pale yellow transverse discal band on a dark brown, or rufous, background on the upperside of the forewing; underside of wings with silver spots ..... tribe HYPNINI *tribus n.*  
(Type-genus: *Hypna* Hübner, 1819, *Verz. bekannt. Schm.*, pt. 4, p. 56; type-species: *Papilio clytemnestra* Cramer, 1777).
- First subcostal vein (V.11) absent or vestigial; second and third subcostal veins (Vs. 10, 9) anastomosing with the costal vein; fourth and fifth subcostal veins (Vs. 8, 7) shorter than the common stalk; the palps relatively short,

erect; basal triangular scales on underside of forewing extending into space 1b; the butterflies being smaller than in the previous tribe, coloured mainly red or brown on the upperside, without a transverse yellow band in the forewing nor silver spots on the underside .....

tribe ANAEINI

(ANAEIDI Reuter, 1896, type-genus: *Anaea* Hübner, 1819).

- (3) Subcostal veins of forewing typically not anastomosing but running free, with veins 5 and 6 typically arising from a short common stalk ..... tribe POLYGRAPHINI *tribus n.* (Type-genus: *Polygrapha* Staudinger, 1887, in Staudinger & Schatz, *Exot. Schmiett.*, vol. 1, p. 182; type-species: *Paphia cyanea* Salvin and Godman, 1868).

Comstock (1961) included in his subgenus "*Polygrapha*" the following taxa: *Anaea suprema* Schaus, "*Paphia tyrianthina* Salvin and Godman, and "*P.*" *xenocrates* Westwood; but if one examines the wing-venation, the basal sensory patch of the palps, and the male genitalia of these species (as figured in Comstock, 1961), it will be seen that they are not congeneric with *Polygrapha cyanea*; hence, if these taxa are to be lumped together, they must represent at least a tribe of the *Anaeinae* and not just a single genus.

- Some of the subcostal veins of the forewing always anastomosing with the costal vein (V. 12), with veins 5 and 6 not having a common stalk ..... 4

- (4) Palps typically somewhat porrect, with a light longitudinal stripe below; the basal triangular scales on underside of forewing delimited by vein 1, not extending into space 1b ..... tribe CONSULINI *tribus n.* (Type-genus: *Consul* Hübner, 1807, *Samml. exot. Schmiett.*, vol. 1, pl. 148; type-species: *Papilio fabius* Cramer, 1776.)

- Palps short, erect (hardly extending above the head), dark below, or with dark and light alternating longitudinal stripes below; the basal triangular scales on the underside of the forewing extending into space 1b ..... 5

- (5) First subcostal vein (V. 11) in forewing typically absent; the palps typically with some long setae on the latero-ventral surface; mid and hind tibiae and tarsi typically spined above and below .....

tribe CYMATOGRAMMINI *tribus n.*

(Type-genus: *Cymatogramma* Doubleday, 1849, *Gen. diurn. Lep.*, vol. 2, pl. 49, fig. 4; type-species: *C. echemus* Doubleday, 1849.)

This group has been incorporated by many authors in the genus *Anaea* (or "*Paphia*") since the days of Doubleday, but it can be distinguished from *Anaea* on the characters already mentioned elsewhere in this paper, such as the differences in the foreleg of the males, in the palps, and in the male genitalia, as well as in the larva (see fig. 12) which is nearer to that of *Consul fabius*

(as figured by Stoll, 1791, pl. 2) than to *Anaea* (see fig. 29, 29a). In addition, the deformed pupa (fig. 12a), which is humped dorsally, is somewhat reminiscent of that of *Hypna*. Westwood (1850) was of the opinion that *Cymatogramma* served as a link between *Consul* and *Hypna* on the one hand, and his "*Paphia*" on the other (the latter genus including species of *Anaea* as well as *Memphis*). The Cymatogrammini appear to comprise the "*verticordia*" group of Comstock's (1961) subgenus *Memphis*", and possibly some members of his "*halice*" and "*arginussa*" groups too; but this will only be known for sure when the early stages of these last two groups become known.

— The first subcostal vein (V. 11) present in the forewing, arising basad of, and free of, the second subcostal vein (V. 10); the palps without long setae on the latero-ventral surface; the mid and hind tibiae and tarsi spined below only ..... 6

(6) The third subcostal vein (V. 9) arising relatively more basad than in the tribe below; the palps typically with alternate dark and light longitudinal stripes below; foreleg of males short, slender, and tapering to a point; the colour of the wings on the upperside red; the inner margin of the forewing straight; the mature larva being naked, without hairs or bristles (see fig. 11) .....

tribe FOUNTAINEINI *tribus n.*

(Type-genus: *Fountainea* Rydon; type-species: *Anaea phidile* Geyer, 1834-7.)

This tribe, judging by the external anatomy of the adults alone, appears to consist of the "*ryphea*" and "*glycerium*" groups of Comstock's (1961) subgenus "*Memphis*".

— The third subcostal vein arising more distad than in the preceding tribe; the palps typically uniformly dark below, with a scattering of light-coloured scales; foreleg of the males longer and stronger, with the tarsus obtusely rounded at the end; upperside colouring of both wings black with blue basal areas, with the inner margin of the forewing emarginate and hooked at the tornus; mature larva covered with hairs or bristles (see figs. 13, 14 .....

tribe MEMPHIDINI *tribus n.*

(Type-genus: *Memphis* Hübner, 1819, *Verz. bekannt. Schmett.*, pt. 3, p. 48; type-species: *Papilio odilia* Stoll, 1780.)

In this tribe I am, for the present, placing the rest of Comstock's (1961) subgenus "*Memphis*"; but when the early stages of the members of this tribe become better known, it may turn out that some of them do not really belong to it.

(to be concluded)